

14

SHRUB ROOTING AND WATER ACQUISITION ON THREATENED SHALLOW GROUNDWATER HABITATS IN THE OWENS VALLEY, CALIFORNIA

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ABSTRACT

Nevada saltbush (*Atriplex torreyi*), *greasewood* (*Sarcobatus vermiculatus*), and *rabbitbrush* (*Chrysothamnus nauseosus* ssp. *viridulus*) root systems were examined in a study to determine the constraints for managing vegetation of Owens Valley, CA, shallow groundwater sites threatened by groundwater pumping for export. A variety of techniques were used, including observation trenches and soil coring. Consistent branching morphology was recognizable for each species through a wide variety of soil types and water table positions. Soil cores extracted to determine root density (length per volume) showed an exponential decrease of roots with depth for all species. Distribution of root density was found to be independent of soil water but parallel to curves of total nitrogen from soil cores obtained from the same sites. The root systems tended to be highly overlapped, suggesting competition for available soil water and mineral nutrients. The three shrub species are apparently well adapted to the poor aeration of soils in shallow groundwater habitats, with the rabbitbrush and Nevada saltbush capable of surviving long-term root system inundation. These species have apparently become adapted secondarily to shallow groundwater sites because the species share numerous characteristics with xeric shrub species of close taxonomic affinity, including aboveground morphology and well-developed drought tolerance. Roots of the three species were found to extend downward when water tables were lowered during field experiments. A maximum root depth, effective for maintaining these shrubs during long-term groundwater decline, was inferred from these data. A relationship of limiting water potential with depth was also determined. In combination, these findings helped formulate a monitoring system to shut down well fields when plant-limiting soil water contents are reached.

INTRODUCTION

Wildland shrubs have come under increasing scrutiny by scientists interested in their management. This is certainly true for the Owens Valley, where we have intensively studied three species of phreatophytic shrubs to

determine how they can be managed in relation to dynamic fluctuations of the water table influenced by the City of Los Angeles' water-gathering activities. These three shrubs: Nevada saltbush (*Atriplex torreyi* [Wats.] Wats.), greasewood (*Sarcobatus vermiculatus* [Hook.] Torr.), and rabbitbrush (*Chrysothamnus nauseosus* ssp. *viridulus* Hall), in combination with two grass species: saltgrass (*Distichlis spicata* [L.] Greene ssp. *stricta* [Torr.] Scribn.) and alkali sacaton (*Sporobolus airoides* [Torr.] Torr.) (authorities according to Munz and Keck 1968), comprise more than 90 percent of the vegetation growing on shallow groundwater zones of the Owens Valley floor. Very little information is presently available from the literature, so the study of these desert phreatophytes represents a new frontier for ecological study.

The Owens Valley climate is arid due to the rain shadow effect of the Sierra Nevada, which intercepts the moist westerly airflow from the Pacific Ocean. The hydrology and associated assemblage of vegetation communities are unique because of the combined effect of the rain shadow and the high level of montane runoff. The arid climate promotes xeric vegetation on the alluvial bajadas surrounding the valley floor, but the valley floor itself supports approximately 38,000 hectares of phreatophytic vegetation.

The Owens Valley has yielded approximately 60 to 70 percent of the water supply for the City of Los Angeles since 1970, exported almost 300 miles to its destination by the Los Angeles Aqueduct. During periods of low precipitation and consequent low runoff, the aqueduct flow is augmented by groundwater pumping. This situation induces water table decline, which isolates the water table from root zones and tends to sharply reduce the cover of phreatophytic vegetation.

For proper land stewardship, impacts due to water table decline on the Owens Valley floor should be avoided because vegetation loss cannot be easily remedied. Saline-sodic Owens Valley floor soils have arisen as a consequence of shallow groundwater in a warm arid climate (Kovda and others 1979). These fine-textured deflocculated soils impair soil aeration and restrict replacement of lost phreatophyte cover by shrubs that grow on the surrounding fan environments. Revegetation of valley floor soils has been poor probably because xeric shrubby species tend to be intolerant to low levels of soil oxygenation (Lunt and others 1973) and because plant establishment in arid environments requires a nearby seed source and a series of consecutive high-precipitation years to foster a "pulse" of germination and establishment (Romney and others 1980).

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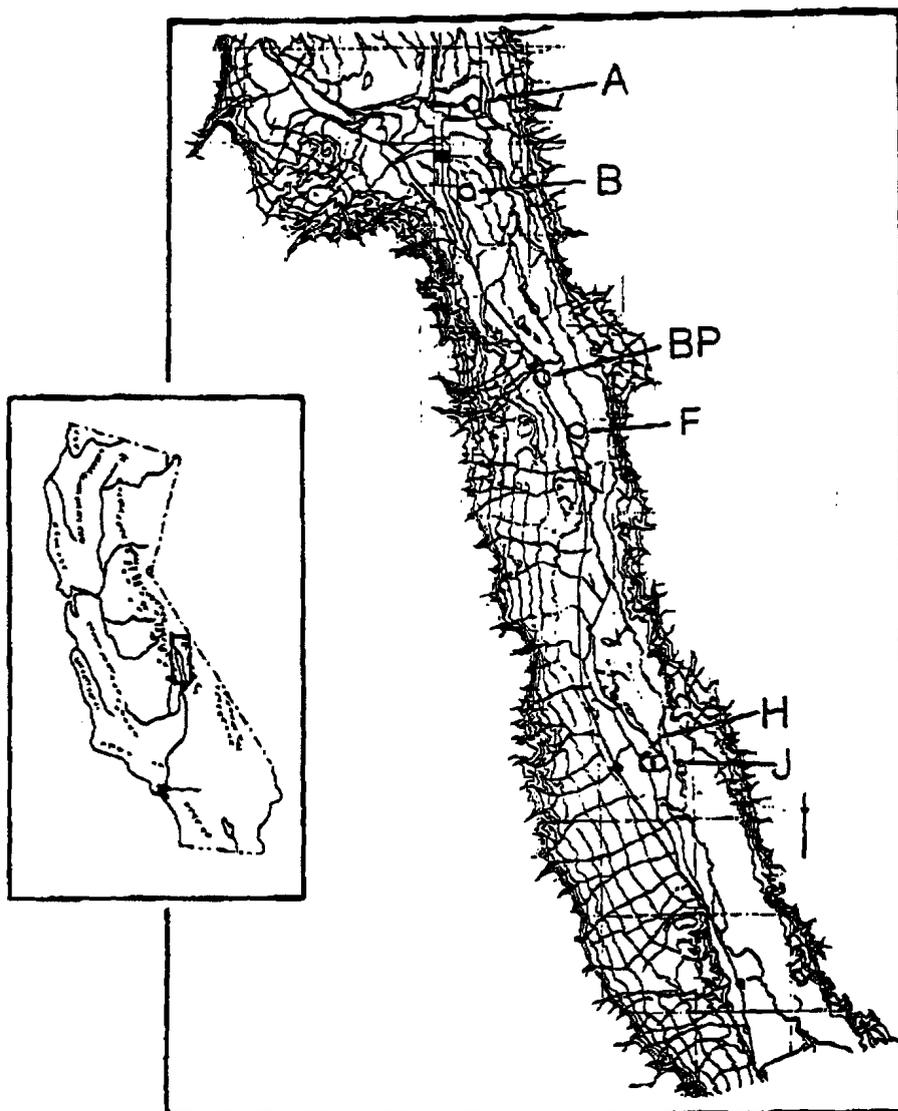


Figure 1—Map of pertinent Owens Valley study sites.

Table 1—Soil properties at Owens Valley study sites. Depth measurements are in meters. The depth studied refers to the greatest depth of the soil trench, units for electrical conductivity are in mmhos/cm corrected to 25 °C, and the broad classification refers to homogeneous or heterogeneous soils. The abbreviations for predominant soil texture: Sa, Lo, Si and Cl, are sand, loam, silt and clay, respectively

Study site	Depth studied	Elec. Cond.		Median bulk dens.	Predom. texture	Broad classification	Watertable depth 4-84
		High	Low				
A	3.6	22.1	1.7	1.50	Sa Lo	Homogeneous	3.3
B	3.0	2.6	.4	1.54	Lo Sa	Homogeneous	2.1
F	3.1	10.6	.5	1.23	Si Lo	Heterogeneous	2.7
H	4.4	20.1	.7	1.50	Cl Lo	Heterogeneous	1.0
J	2.6	10.0	.8	NA	Cl Lo	Heterogeneous	1.0
BP	(no soil trench or chemistry)				Lo Sa	Homogeneous	3.3

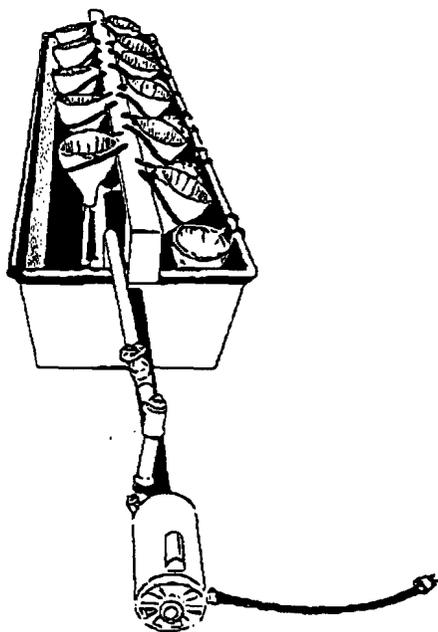


Figure 3—An elutriator for separating roots from soil. Water flow was provided by the pump in the foreground. Soil cores were placed in the funnels and the nets on the stock tank sides strained the roots from the water flowing over the funnel rims.

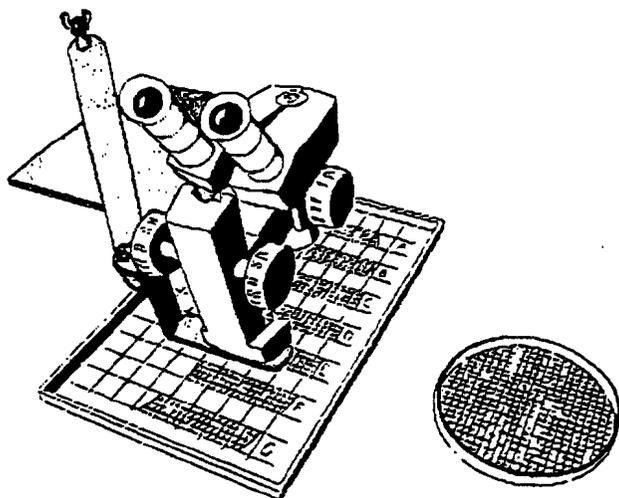


Figure 4—Microscope and grids for estimating root length. Two sizes of pans were used depending upon the amount of root material in the sample. To achieve a random sample, the microscope swing arm was moved to each of seven positions without reference to the root tissue beneath. On the larger pan, readings were obtained from each of seven separate fields, A through G.

The roots were arranged randomly in a water bath on the grid field, and the intersections with grid lines of roots that appeared "live" according to set criteria were counted. These criteria were determined by observation of both fresh and dried roots known to be alive prior to collection. Random distribution was achieved by placing the roots in a water bath on the pan and then agitating the water to provide even dispersal. Counts under seven microscope fields (10x) were totaled and converted to length in meters using an empirically determined factor for each grid field.

Soils of sites B and H were studied more intensively than at the other study sites. Total nitrogen and phosphorus per 0.3-m depth increments were analyzed to compare with depthwise rooting density data. Soil samples for these determinations were obtained at three random locations within each of the study sites. These analyses employed modified Kjeldahl digestion on air-dried soil samples. Total nitrogen and phosphorus concentration were then determined by colorimetric analysis (molybdate for total phosphorus—Olsen and Sommers 1982; and sodium salicylate for total nitrogen—Bremner and Mulvaney 1982).

Results—Data derived from coring were expressed in meters of root per cubic decimeter of soil (equivalent to 0.1 cm/cm^3), termed "root density," following the convention adopted by Nye and Tinker (1977). The statistical distribution of root density data was found to lack normality, probably because root initiation is, in effect, a random process followed by proliferation, which is an exponential process (St. John and Hunt 1983). The appropriate statistical distribution to describe this process is a negative binomial, which can be normalized by adding 1 and taking the base 10 logarithm (Anscombe 1949). One is added to the root density to ensure that the logarithmic values remain positive. This transformation permitted use of parametric statistics to compare and statistically model root-core data.

Analysis of roots by the Newman (1966) method did not determine the actual living root fraction because criteria chosen to represent living roots were confounded by residence time of shed root material before decomposition, a problem that was significantly more pronounced in dry soils. An attempt to solve this using water soluble dyes on fresh root material (Ward and others 1978) failed to differentiate between living and dead roots due to the uptake of stain by dead and decomposing root tissue as well as by roots that had obviously been living when sampled. Many roots that appeared living according to the criteria failed to absorb the stain. Another attempt at identifying living roots by using tetrazolium chloride also failed. The living roots examined had insufficient respiration to activate the expected color change, while microbial respiration within decomposing roots activated the dye to a characteristic bright pink. Although beyond the scope of this investigation, further work to refine possible staining techniques to identify living roots is warranted, since a measure of actual living root density, rather than an approximation, is required for many modeling applications.

In all cases, root density was seen to decrease exponentially with depth. Within homogeneous soils, this distribution could be modeled accurately as a line due to

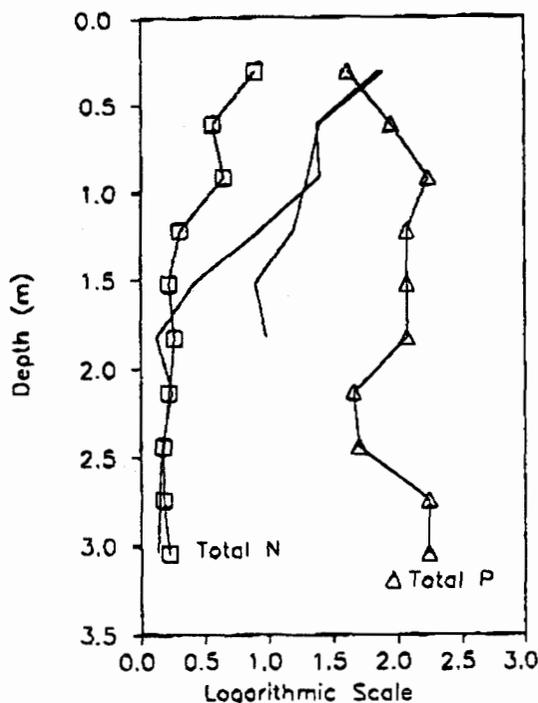


Figure 7—Average root density and total nitrogen and phosphorus at site B. The nitrogen and phosphorus data were collected in August 1987 from three random locations and averaged following transformation ($100 \times \text{base } 10 \text{ logarithm of weight percent plus } 1$), which permitted comparison at the same scale as the transformed root density. Unweighted average transformed root densities for shrubs ($n = 10$) and grass plots ($n = 2$) are plotted as two lines without symbols. The shallower line represents results from sampling in January 1984, before water table drawdown. The deeper line is for sampling during January 1987, following approximately 3 years of artificial drawdown. Note how root density tends to parallel the line for total nitrogen concentration.

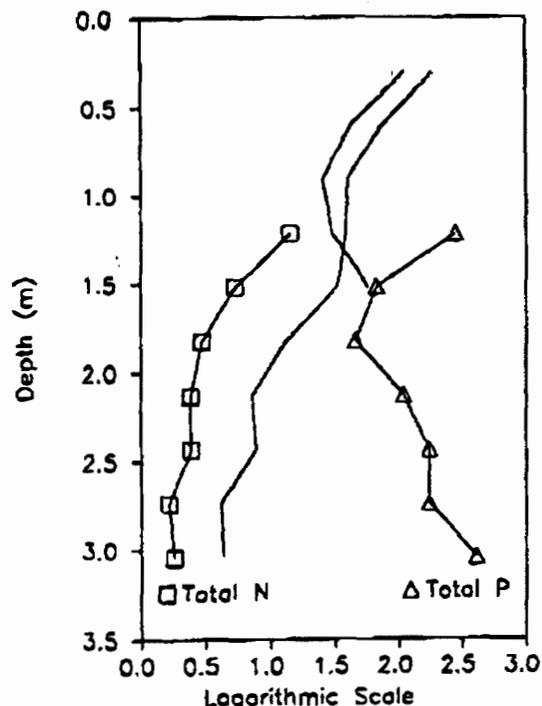


Figure 8—Average root density and transformed total nitrogen and phosphorus at site H. Nitrogen, phosphorus, and root density data are plotted as in figure 7, except for depths above 1.0 m where concentrations were greater than 5 on the logarithmic scale. The far greater near-surface N concentration was probably due to the presence of the nitrogen-fixing perennial legume wild licorice (*Glycyrrhiza lepidota*). The root densities are unweighted averages of transformed root density for shrubs ($n = 8$) and grasses ($n = 1$). The deeper portions of January 1987 root density (deeper line) are remarkably parallel to the line for total nitrogen concentration.

hypothesized to have been unavailable. Nitrogen in the horizons deeper than the top meter of soil were from five to six orders of magnitude less.

Discussion—Why do roots of these shrubs show an exponential decrease of density with depth? As a factor influencing depthwise root density, soil water, by itself, can be dismissed since soil water contents typically increase with depth due to subirrigation from the shallow water table. Soil chemistry, aeration, or perhaps gross root system morphology, whereby more root buds are found near the surface, may also influence the depthwise distribution of roots.

As indicated by curves in figures 7 and 8, the concentration of total soil nitrogen correlates well with depthwise root density. Exponential distribution of roots may occur simply because the Owens Valley soils tend to have low nitrogen contents, except within the uppermost horizons.

In the general case, nitrogen in desert ecosystems has been found, like root density, to decrease exponentially with depth (West and Klemmedson 1978).

The correlation of root density by soil nutrients is not unique to the Owens Valley floor shrub species. Root density within specific soil zones for a variety of species has been positively correlated to soil nitrogen in numerous studies (for example, see Russell 1977). The interrelationship of water and nutrients is a fruitful area for study, especially by simulation. Analysis of metabolic costs for root production and maintenance versus benefits in the form of water and nutrient uptake led Hunt and others (1987) to conclude that root surface area for the semiarid species *Agave deserti* was adjusted primarily for nutrient uptake and only secondarily to supply water.

All other factors that may influence root growth and also change with depth apparently play a reduced role in

Table 4—Mixed root density of alkali sacaton and Nevada saltbush by radial position—site A. Data were obtained by coring a trench face during late September 1983. The columns are radial distances in meters away from the axis of the Nevada saltbush. The rows represent depths below the ground surface in meters. By two-way analysis of variance, no statistical difference existed for position relative to the shrub canopy. The saltbush specimen measured about 1.5 m in diameter with a leaf area of 2.7 m at the time of sampling. Although the lowest root density for the near-surface depths occurred within the dripline of this shrub, this phenomenon was absent for two other data sets obtained for similar Nevada saltbush/alkali sacaton associations at this location

Depth	Radial distance from shrub axis (m)								row \bar{X}
	0.3	0.6	0.9	1.2	1.5	1.8	2.1	2.4	
0.3	1.43	1.61	2.14	2.58	2.33	2.13	2.14	2.23	2.07
.6	1.21	2.18	2.02	2.89	1.80	1.72	1.82	1.92	1.94
.9	1.51	1.75	2.02	1.89	1.77	1.67	1.49	1.75	1.69
1.2	1.41	1.28	1.43	1.25	1.33	1.40	1.21	1.42	1.34
1.5	1.34	1.17	1.02	1.36	1.32	1.41	1.40	1.37	1.30
1.8	2.11	.64	1.16	1.01	1.13	1.11	1.91	1.14	1.28
col \bar{X}	1.50	1.44	1.63	1.83	1.61	1.57	1.66	1.64	1.60

possible to make inferences about the relative mixture of roots of the two species using the techniques employed. The larger suberized roots of Nevada saltbush could be distinguished from alkali sacaton, but such large roots made up only a very small proportion of the total sampled root length.

Discussion—Although a large degree of variability in spacing of Owens Valley floor plants may be encountered, undisturbed shallow groundwater sites dominated by shrubs commonly have intershrub distances of less than a crown diameter (approximately 1.5 m). Therefore, the data of root density relative to shrub position indicate that the wide radial distances explored by the three shrub species induce a relatively intense overlap of their root systems.

Overlapped root systems imply intensive competition among individual plants within and among species. We have anecdotal evidence that the overlapped root systems typical of the shallow groundwater sites compete for the available soil resources. At sites B and H, simple visual comparison of shrub growth, where neighboring shrubs and grasses were removed to an adjacent portion of the enclosures where the vegetation was left untreated, revealed that plants relieved of neighbors grew noticeably more vigorous. This same phenomenon can be observed throughout the Owens Valley floor where shrubs grow more robustly along unpaved roadways than on adjacent undisturbed ground.

To understand overlapped root systems and competition for nutrients and water in desert environments, a thorough comparison of the soil and edaphic conditions on a range of environments is necessary. Although belowground competition due to root system overlap is thought of as being a condition typical of arid environments, Barbour (1973) cautioned that this generality

cannot be applied in all cases since in many arid environments, particularly those with the lowest available water, root overlap does not occur. Nevertheless, root overlap is a common feature of arid and semiarid regions in North America. Examples include the Sonoran Desert (Cannon 1911), Southern California chaparral (Hellmers and others 1955), and Mojave Desert (as may be inferred by competition data collected by Fonteyn and Mahall 1978).

Plants tend to optimize root/shoot ratios (Brouwer 1963, as cited in Russell 1977). Since root growth must remain in balance with greater aboveground production afforded by the input of water from groundwater, it is logical to expect intense overlap of the root systems of Owens Valley floor plants. The degree of root system overlap might therefore be best viewed as a continuum, which occurs to an increasing degree as soil water becomes less limiting and as soil nutrients therefore become more limiting.

Although not reported here, root distribution was also studied within heterogeneous soils of the Owens Valley floor (Groeneveld, unpublished data). Although root density within heterogeneous soils tends to be determined in large part by contrasting physical and chemical properties of soils within mound and microplaya formations, root systems were inferred to be strongly overlapped because both interspecific shrub associations and belowground roots tended to occur in clumped distributions on and within the mounds.

Mixed species root density surrounding Nevada saltbush within crowded alkali sacaton at site A (table 4) was much greater than from site BP, which lacked grass cover (table 3). Measured grass root densities were greater than for shrub roots at each of eight study sites (of the total 11 sites developed) where this comparison could be made (Groeneveld, unpublished data). This held true even when the aboveground grass canopies were comparatively sparse.

The largest transformed root density value of table 4 is 2.89, which corresponds to 775 m/dm³. This value is excessive when compared to values presented in the literature. For example, Dittmer (1937) estimated winter rye to have over 5,000 m of roots per plant. These results confirm that the sampling also recorded dead roots. The largest untransformed value for root density recorded at site BP (table 3), by contrast, was only 12 percent of the maximum recorded at site A. The smallest transformed value for Nevada saltbush root density recorded at site BP (table 4) is 0.64, which corresponds to about 3.4 m/dm³. This confirms trends reported in the literature where grasses have greater intrinsic root density and turnover of roots than woody plants. Because of wide lateral rooting of the shrub species compared to the grasses, it is not possible to say whether the ratio of root surface to leaf area is higher in grasses than in shrubs when only viewing isolated portions of the root systems by coring. Due to their lack of secondary development (Esau 1965), roots of grasses are limited to the extent with which they may explore the soil, and so are generally limited to the zone beneath the immediate surroundings of the aboveground shoots. Shrubs, by contrast, are capable of growing much greater lateral distances from the aboveground shoot and, therefore, of utilizing water and nutrients from a much larger volume of soil.

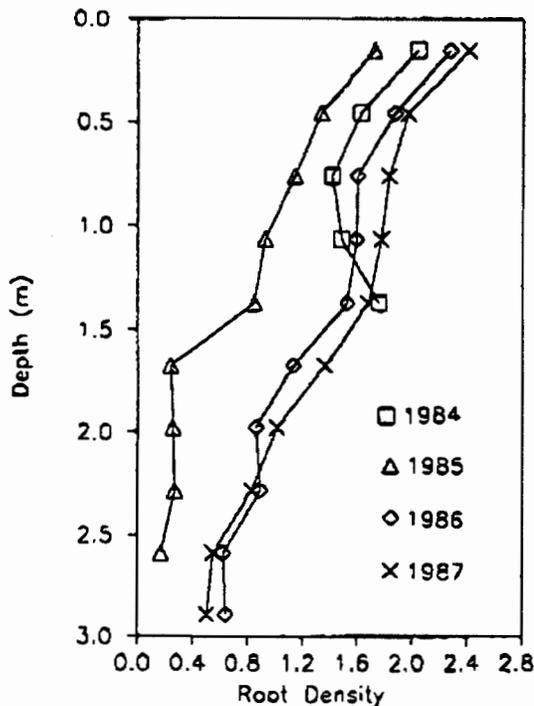


Figure 10—Progressive annual samples of root density samples—site H. Note the increasing root density as sampling progressed. Compared to site B data (fig. 9), the greater depth-wise growth suggests promotional effects of fine-textured soil. Water table levels for the sampling periods were 1.0 m just prior to the 1984 sampling, 3.4 m in 1985, and 4.7 m in 1986 and 1987.

Lower root density at site B (fig. 9) indicates a reduced potential for downward rooting compared to site H (fig. 10). Untransformed root density at 3.0 m at site B ranges between 0.15 to 0.20 m/dm^3 at 3-m depth for both January 1985 and 1986. Compared to high near-surface, untransformed root densities of 70 m/dm^3 , such low root density at 3-m depth by itself may be inadequate to supply the canopy during periods of soil water deficit if the remainder of the horizon has reached limiting water content.

A comparison of root density data January 1986 to January 1987 from site B (fig. 9) illustrates a major problem in judging root density by appearance only. The values for much of the soil horizon are nearly identical for these samples. Soil water extraction may have halted microbial degradation of nonviable root tissue.

Results of the analysis of probable maximal depth of effective rooting are presented for site H, where pumping achieved the greatest drawdown and depth to water (fig. 11). Even though the water table was lowered approximately 2.0 m less than that achieved at site H, site B data indicated the same maximal rooting depth (data not shown). Unlike site B, the site H data for January 1986 and 1987 were quite different; the root density

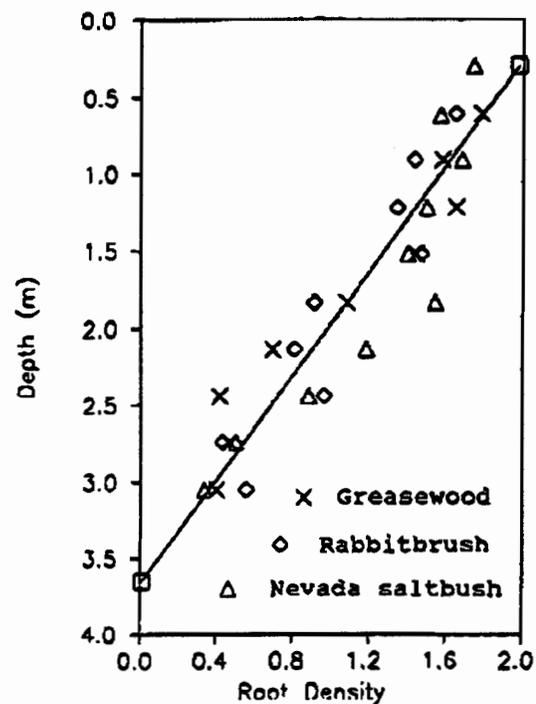


Figure 11—Predicting maximum effective rooting depth—site H. The data are per-species arithmetic averages of transformed root density sampled in January 1987. The line was fitted from an unweighted average of the values shown, yielding a correlation coefficient of 0.99. The maximum effective rooting depth predicted is 3.6 m. The water table was at about 4.7 m at the time of sampling.

within site H soils increased. Lines fitted using average values of root density per species indicated, for both sites, that the probable maximum effective depth of rooting was approximately 3.6 m.

Discussion—The rooting depth limit is an important constraint for management of these three shrub species. The maximal depth can be used to define the bottom of the effective root zone of these species, which then allows evaluation of the plant available water within the rooted soil volume.

The fact that data from two sites with very different soils showed similar maximal root depth (about 3.6 m) suggests that a maximal effective depth of rooting may be an intrinsic factor for these species when growing on Owens Valley floor soils. These results also imply that the combination of slow drawdown rate and coarse soil of site B met the requirements for downward growth. Where soils are excessively coarse, such as the cobbles, gravels, and sands often found lining active stream channels, insufficient water films may be retained to maintain the plant water balance, fund deeper root growth, or maintain a gradient to encourage downward rooting (Groeneveld and Griepentrog 1985).

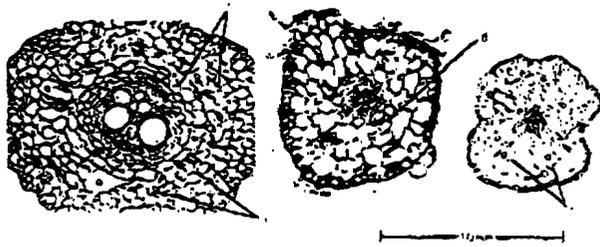


Figure 12—Photomicrographs of root cross sections. Nevada saltbush grown under flooded (left) and nonflooded (center) conditions and a containerized rabbitbrush root (right) treated to induce poor aeration. Features that can be seen in the cross sections include: (a) aerenchyma with fragments of lysed cell walls evident; (i) intercellular spaces in the cortex; and (d) druse crystals in Nevada saltbush cortex. Note the size difference between the xylem lumina in the flooded and nonflooded Nevada saltbush.

Under the microscope, it was apparent that both Nevada saltbush and rabbitbrush roots had developed lysigenous aerenchyma under flooding (fig. 12). These air spaces arise in the cortex of primary roots due to lysis of cell walls induced by endogenous ethylene concentrated as a "water jacket effect" under flooded conditions (Konings 1982). Numerous workers have identified that aerenchyma function to reduce intercellular resistance to oxygen diffusion (Williams and Barber 1961; Coutts and Armstrong 1978).

The flooded greasewood, by contrast to the Nevada saltbush and rabbitbrush, had experienced severe dieback with less than 5 percent of the original canopy still viable. Root systems on these plants were dead and undergoing decay. Similarly, Ganskopp (1986) found greasewood to be quite tolerant of relatively low soil oxygen but intolerant of prolonged flooding, as implied by its growth and development relative to shallow water tables.

Microscopic examination of the roots of all three shrub species growing under well-aerated field conditions failed to locate aerenchyma in primary tissue. These roots were much smaller in diameter than flooded roots and cross-sectional areas of the xylem lumina in these roots were smaller by two orders of magnitude (fig. 12). The hypertrophied xylem seen in flooded roots may compensate for the much-reduced root surface area under flooding compared to the canopy size.

Primary roots of all three shrub species grown under relatively poor aeration within the pots also developed aerenchyma, even though primary roots of these plants were similar in gross appearance to roots grown under conditions of relatively high aeration. Aerenchyma were consistent in size relative to the cells within container-grown roots, but tended to occupy more of the cross-sectional area of the roots (fig. 12).

Observations of root systems of Nevada saltbush and rabbitbrush in the dewatered trench adjacent to the

flooded site indicated that the well-differentiated root systems adapted to exorrhizal oxygenation failed to survive flooding that occurred when the water table rose during the period prior to trenching. The height of the inundating water table was easily discernable in the coloration of the roots. In appearance, flooded roots were intact and still connected to viable tissue above the previous water line but were blackened, shriveled, and obviously nonviable. The blackened appearance may be due to exclusion of oxygen because the horizontal zone separating living roots from their flooded former extensions was accompanied by a soil color shift (gleying), which occurs under reduced redox potential.

Discussion—Lack of survival of mature root systems below the water table for both flooding-tolerant rabbitbrush and Nevada saltbush refutes a common concept about phreatophytes: Such species send roots below the water table to tap groundwater (for examples, see Meinzer 1927; Robinson 1958; McQueen and Miller 1972). As the observations of rabbitbrush and Nevada saltbush have shown, few phreatophytic species may readily penetrate the water table very deeply. This is because of the presence of toxic compounds under anaerobic conditions (Rowe and Beardsell 1973), the replacement of flooded root systems by primary tissue (only the cortex of primary tissue may develop aerenchyma), and also poor soil penetrability that may be hypothesized to limit downward extension of spongy aerenchymatous roots. It is far more likely that water tables may periodically inundate aerenchymatous roots that lie within a dynamic zone where water table fluctuation occurs. Presence of aerenchyma-containing roots within such a zone was observed for both Nevada saltbush and rabbitbrush during trenching and root observations at site H.

Development of aerenchyma has been well documented in the literature for wetland plants, and has been thought by some researchers to represent an adaptive response (for examples see Drew and others 1979; Kawase 1981). As an adaptive response, development of aerenchyma in the three shrub species, in concert simply with tolerance for low soil oxygen, may permit these species to occupy alkali sink habitats where competition is relaxed due to exclusion of xeric species that typically have high soil oxygen requirements (Lunt and others 1973). Although greasewood developed aerenchyma under conditions of impaired aeration, development of these features may not confer survival during long-term flooding.

Both rabbitbrush and Nevada saltbush have taxonomic affinity with species (and subspecies, in the case of the former) that inhabit predominantly xeric sites (Hall and Clements 1923; Munz and Keck 1968). Xeric ancestry combined with such marked xeric ecophysiological characteristics as leaf shedding under intense water stress and the ability to deplete soil water to below -4.0 MPa suggest that these species have adapted to arid shallow groundwater habitats secondarily. Relaxed competition afforded by such sites may have been the driving force for this adaptation (Groeneveld and Crowley 1988).

plant stress, the water potential should theoretically be the same throughout the rhizosphere. However, when grab samples are obtained to determine water potential by filter paper or other ex situ technique, the measurement characterizes only the bulk soil and not the rhizosphere. Because, at limiting water contents, exponentially increasing resistance to soil water movement retards water flow to the root sink, three-dimensional "islands" of water are stranded in the soil volume not penetrated by roots. If insufficient root density exists to grow into and exploit these zones of relatively available water, even if plant extraction has reached the limits afforded by osmotic adjustment in the shoot, the apparent "bulk" water potential will be greater than the water potential measured under conditions where roots ramify thoroughly within the soil volume. This condition was demonstrated for an ex situ method, the filter paper technique, but is equally valid for in situ measurement of soil water potential by instruments such as soil psychrometers or soil resistance blocks.

SUMMARY AND DISCUSSION

An understanding of the ecology of the three shrub species, Nevada saltbush, rabbitbrush, and greasewood, has been gained from the study of their roots that is far greater than would have been afforded simply by studying their aboveground structures and ecophysiology. As a practical benefit, the insights gained through the study of roots have permitted the development of a system of monitoring and management to preserve the vegetation comprising these species where it forms the ground cover within well fields.

Within the arid Owens Valley, shallow water tables permit vastly greater plant production compared to adjacent xeric habitats. However, deleterious factors are also concomitant with shallow groundwater—poor soil aeration, salinity, and sodicity. These three shrub species are capable of withstanding highly salt-affected soil, poor aeration, and with the exception of greasewood, flooding. Despite their phreatophytic habits, these species are also remarkably drought tolerant and respond to water deficit in the same manner as the xeric species of close taxonomic affinity. This suggests a secondary adaptation to shallow groundwater sites driven, perhaps, by the advantages of increased production and exclusion of nonadapted, but potentially competitive, species.

Shallow groundwater habitats are, by definition, much wetter than xeric habitats. Subirrigation tends to buffer phreatophytic plants from the extreme swings of available soil water that occur in xeric habitats as a consequence of infrequent precipitation. Therefore, soil water content by itself is probably not a limiting factor for plant growth on most naturally occurring, unaltered shallow groundwater sites.

The root data suggest that, of many factors which may influence root distribution, the soil nitrogen or, perhaps, some cofactor may play a dominant role. Both roots and nitrogen decrease with soil depth as an exponential relationship.

The balance between root extraction and capillary replenishment from the water table frequently induces

a clearly demarcated zone in the soils of Owens Valley shallow-groundwater sites—dry above and wet below. Under this type of dynamic equilibrium, it can be hypothesized that, because of its distribution, nitrogen (or a cofactor) will tend to be only poorly available until sufficient water becomes available in the near-surface horizons to permit absorption. Thus, even though the Owens valley shallow-groundwater vegetation is phreatophytic, precipitation should have a strong influence on productivity. Such promotional effects on valley floor vegetation by precipitation were documented during related studies accomplished concurrently to those reported here (Sorenson and others 1989a). Also, models formulated from data collected at sites B and H to simulate the response of transpiration and leaf area to either retained soil water or precipitation have clearly demonstrated a synergistic promotional effect by precipitation (Welch 1988).

Due to water available from the water table in excess of that supplied by the arid climate, valley floor plants grow in relatively dense stands and this induces intense overlap of root systems. At least by observation, the close proximity and relatively high production of plants on shallow groundwater habitats induces competition. The cycling of nutrients and water and their effect upon competing plants within these habitats is an especially fruitful area for further study—especially by simulation, since the soil plant system is relatively simple and the sources and sinks for nitrogen and water are quantifiable.

Rooting data gathered for the important Owens Valley floor species, including these shrubs, have been crucial for devising a monitoring system using paired vegetation transects and soil water measurements. Data from monitoring permits projection of plant water requirements through a growing season and estimation of plant-available soil water based upon an extension of the soil water characteristic function described in Sorenson and others (1989b). Utilizing these calculations, groundwater pumping is then curtailed when soil water content is projected to be insufficient to maintain the vegetation through a coming growing season. Recovery of the water table to the root zone then follows during a span of from 1 to several years, depending upon the amount of runoff from the Sierra Nevada. Managing a hydrobiotic system in this manner essentially requires exploitation of the wide range of tolerance of the vegetation—especially drought tolerance.

The root studies have provided two important relationships that have been included in the monitoring/well shutdown scheme. The maximum effective root depth provides the lower boundary for calculating available water. Since the decrease of roots with depth does not permit extraction of all water in the bulk soil down to the limits imposed by the plant's physiology, the empirical relationship for depthwise limiting water potential (fig. 13) has been used to decrement estimates of plant-available water by depth.

For the monitoring/well shutdown scheme to successfully preserve the existing vegetation cover on the Owens Valley floor, sufficient soil water reserves must be built into the calculations to prevent biasing for vegetation impacts, since water tables require variable, but

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potentially long, periods to recover. With the competing interests of Inyo County and the City of Los Angeles, the former toward preserving and enhancing the Owens Valley environment and the latter toward acquiring its water, a great deal of reliance has been placed upon the monitoring system. The principle for monitoring and well shutdown has been included as the basis for a permanent agreement for valley management. The interests of Inyo County are best served by a generous reserve of soil water to protect the plant cover, and those of the City by just enough of a reserve to avoid impacting and thus, perhaps, changing the vegetation permanently. Fortunately, through the flexibility built into the agreement, this scheme has the potential for adjustment to achieve the clearly stated objective of preserving the existing vegetation cover.

Operation according to the monitoring/well shutoff scheme may induce types of stresses upon the valley floor plants not yet documented. During multiple-year cycles of above-normal Sierra Nevada runoff, regional water tables may rise and flood root zones of valley floor vegetation. During drought, the extraction of groundwater to augment a decreased export of surface water necessarily lowers the water tables within well fields and induces multiple-year periods of increasing soil water deficit. Since climatic variables remain relatively stable over time, the driving variables for long-term stress of the vegetation involve soil water processes that are strongly affected by extraction and export of groundwater. Therefore, the key to the maintenance and recruitment of vegetation within well fields will be the plasticity of root systems and their capability to withstand a wide fluctuation of soil conditions. For this reason, the study of root systems of these intriguing plants must continue.

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